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JUVENILE KELPS AND THE RECAPITULATION THEORY. I.

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I. THE DEVELOPMENT OF CERTAIN KELPS

A. *Renfrewia*[1]

FOR the preparation of a former article (Griggs, '06) on Renfrewia the writer had no very young plants, but during the summer of 1907 he was enabled to collect a full series at the Minnesota Seaside Station, Port Renfrew, B. C. This material is of interest for the study of the development of this, the most primitive of the kelps in comparison with the more complex forms.

The smallest specimen found, which measures a trifle less than 4 mm. (Fig. 1), is not certainly determinable. But one 13 mm. long (Fig. 2) had already developed a peculiar swelling of the basal region which characterizes the young plants. The primitive disc of most kelps and of Renfrewia up to this age is rather flat and sharply separable from the stipe, which ascends cleanly without tapering from the top of the disc. In Renfrewia, however, the basal region of the stipe (the region which in other kelps develops hapteric outgrowths) increases in size. As the plant grows this swollen region becomes more prominent till in plants 8 cm. long (Fig. 11) the

[1] Since publishing the original account of *Renfrewia parvula* in 1906 I have found that it is apparently conspecific with Setchell's ('01) *Laminaria ephemera* earlier described from the California coast. Accordingly Setchell's name replaces mine and the plant becomes *Renfrewia ephemera* (Setchell). Cf. Setchell, '08 b.

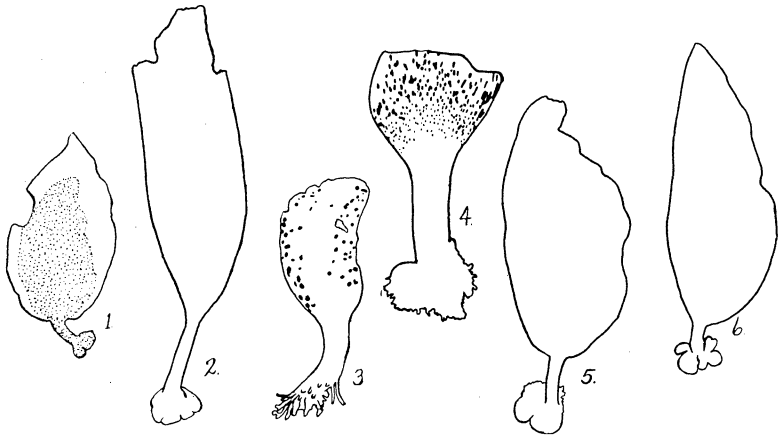


FIG. 1. Renfrewia, 4 mm., shading shows the position of single and many-layered areas in the lamina, holdfast without basal cone.

FIG. 2. Renfrewia, 13 mm., lamina many-layered throughout basal cone beginning to appear.

FIG. 3. Lessoniopsis, 1.1 mm., lamina about four-layered, spots already shown in the cortex, holdfast not developed, plant apparently anchored by filaments.

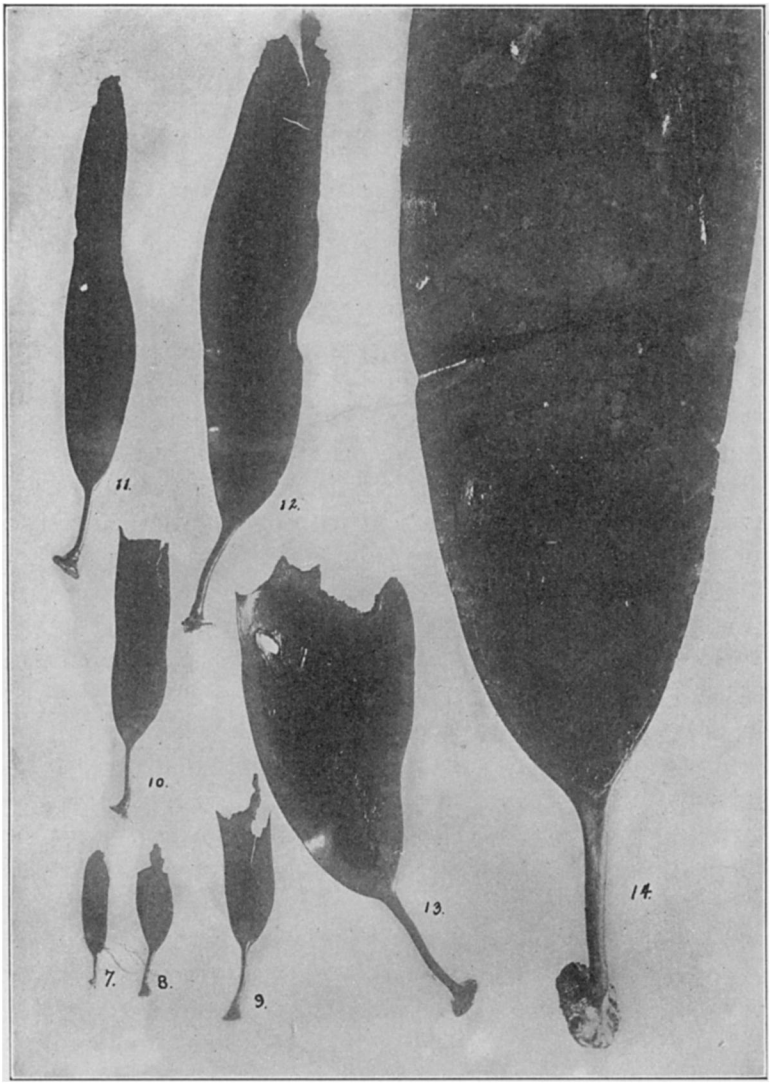
FIG. 4. Lessoniopsis, 2.3 mm., spots in the lamina larger and more evident distally, but still small near the transition region, indicating that growth is already localized, primitive disc developing at base of stipe.

FIG. 5. Hedophyllum, 2.3 mm., showing the much-lobed primitive disc.

FIG. 6. Hedophyllum, 10 mm., lobes of primitive disc grown into the primitive hapteres.

holdfast is an almost straight-sided cone 5 mm. in diameter and of about equal height. Though apparently insignificant this character makes it easy to pick out Renfrewia from other kelps while yet very small. So far as the writer is aware it is not present in any other kelp.

After the plant has reached about a decimeter in length the basal cone ceases to increase and later is lost in the growth of the stipe (Fig. 12). At the same time the disc begins to enlarge and spread out on the substratum, giving a firmer hold for the increasing lamina above. This enlargement is clearly in the region of the primitive disc and not in the conical basal swelling above, which remains part of the stipe. These two tendencies of growth working together usually cause the sharp distinction between the holdfast and stipe to reappear, and in plants more than 15 cm. long the conical base is seldom prominent (Fig. 13). In adults the disc becomes very flat and thin by its continued extension (Fig. 14).



FIGS. 7–11. Renfrewia, series of young plants showing the development of the basal cone. Four fifths natural size.

FIGS. 12–13. Renfrewia, older plants showing the gradual disappearance of the basal cone with increase in size. Four fifths natural size.

FIG. 14. Renfrewia, base of an adult plant, fruiting area extending over almost the entire lamina, its margin indicated by shadows here and there, holdfast showing primitive hapteres. Four fifths natural size.

Some speculations as to the nature and significance of this cone may be of interest. Of all the kelps Renfrewia and Cymathere are the only ones in which the mature holdfasts are restricted to the primitive disc region. In the development of the latter genus, as traced by the writer ('07), there is no indication of such an organ as can be seen by an inspection of the figures then published. Phyllaria and Saccorhiza differ in their holdfast characters from all the other genera. Instead of putting out hapteres directly from their stipes they develop bulbous "rhizogens" which form ring-like collars around the stipe. From these the hapteres are formed by unequal growth along their margins. Though the rhizogen in both genera is separated from the primitive holdfast by a distinct interval on the stipe, it is essentially similar to the basal cone of Renfrewia which we may consider as an incipient rhizogen. This would indicate some leaning of Renfrewia toward the Phylariatæ; but its paraphyses are of the typical clavate form not at all similar to the linear ones of that group. Whether this basal cone is a nascent organ representing the beginning of the holdfast or is a vestige of a Saccorhiza-like rhizogen is a puzzling problem. At some stage in their history the rhizogens of Saccorhiza and Phyllaria probably passed through this condition and remained for a longer or shorter period without further development. On the other hand, the obscuring of the cone in Renfrewia when adult might suggest a vestigial organ. Perhaps the best hypothesis is that Renfrewia was cut out from the main advancing phylum of the kelps, isolated and fixed, at the stage where the tendency to form a secondary holdfast was just beginning to manifest itself.

The tissues of the many-layered lamina of Renfrewia are apparently acquired after the fashion of other kelps, but in Renfrewia the many-layered lamina begins its development in smaller plants than in the Phylariatæ including Cymathere. Even in the smallest specimen (Fig. 1) there is only a small portion of the one-layered blade remaining around the edge of the lamina. In the

13 mm. specimen (Fig. 2), the whole lamina is many layered without any signs of the one-layered portion persisting around its edges. Apparently the embryonic lamina is almost wholly transformed into the adult blade. Like the adult, these young plants are light colored and delicate in texture. They are narrowly elliptical in shape, cuneate at the base and rounding to the apex when not badly abraded.

Except for the basal cone of the stipe young plants 15 mm. long in all characters are like the adult. The adult is larger but the proportions remain the same. Even in the histology there is probably very little differerence, for, as described below, Renfrewia develops very imperfectly the complex tissue system which characterizes the higher kelps. What differentiation of tissues appears is probably present long before adult size is reached. Were it not for their reproductive maturity it would be difficult to demonstrate that the adults were mature and not merely larger juvenile forms (Figs. 16, 17); and they have been mistaken by competent observers for juvenile forms of some other kelp.

B. *Lessoniopsis*

Lessoniopsis is a monotypic genus ranging along the Pacific coast from California to Vancouver Island. It was founded by Reinke ('03) to receive *Lessonia littoralis* Farlow and Setchell (see Setchell, '03) which differs from Lessonia in the marked dimorphism of the laminæ, as described below.

The juvenile forms of Lessoniopsis are extremely abundant during July and August at the Minnesota Seaside Station. They grow in clumps of many individuals of all ages. As often as not these clumps start upon the stipes of other kelps, so that one can obtain many hundred specimens simply by cutting off a few old Laminaria stipes. Though the mature plants are often single, it is not at all unusual to find several large plants fused together, as was noticed by Reinke. The reason for this habit of growth of the sporelings is a matter of some in-

terest. There is no difference, as far as the writer is aware, between the fruiting habits of this and other kelps. In quiet water the fragments of any fruiting lamina torn off by the waves might lie undisturbed on the bottom and the spores might germinate close to the point of liberation. But this kelp is a cumaphyte growing exclusively in the strong surf, and it is in surf-scoured situations that the young plants are found best developed. This would lead one to look for some method of basal branching or possibly budding of new laminæ from the holdfast, as is known in a few kelps which have "rhizomes." But though hapteres and stipes are occasionally so completely grown together as to appear branches of one plant, no evidence of such branching in the young plant has been observed and the writer must conclude that the clusters are due to starting of many spores at one point.

The young plants forming these clumps are thickly splashed with checks of dark brown on the lighter color of the body of the lamina. This is most conspicuous in plants about 10 cm. long and is clearly brought out in the photographs (Figs. 15, 21). As they grow older the spotting tends to disappear, but traces of it can usually be found in specimens of any age. No other kelp of the region is similarly marked except Pterygophora, in which the spots when present are much less distinct. As this appearance arises very early it is of the utmost service in identifying the plants while yet too young to have developed any characters of the adult.

The smallest specimen found (Fig. 3) measured about 1.1 mm. in length. It was attached to the hapteres of another plant of the same species twenty or thirty times as long. When loosened from its hold it came away with a mass of filamentous material which completely enveloped its base. In this tangle there was a considerable portion of foreign matter; but the appearance of the finer strands was that of a protonema-like felt organically connected with the young kelp which seemed to spring from it like the gametophore of a moss. On teasing this away it was seen that the primitive disc had not yet developed.

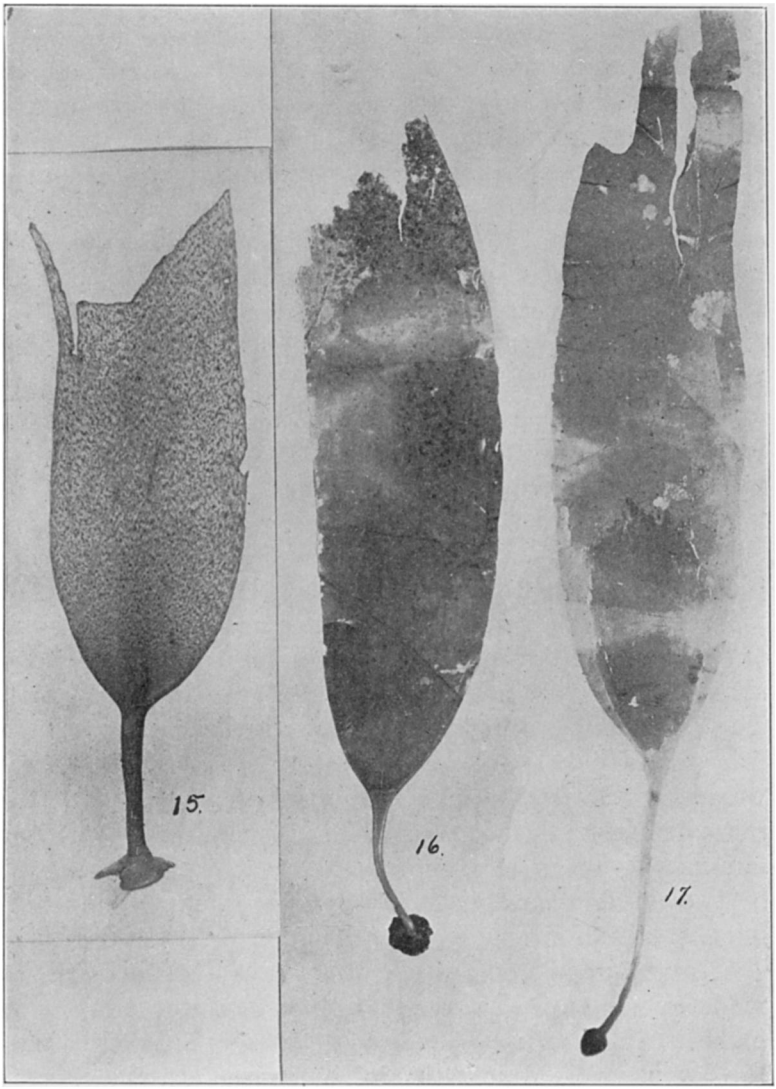


FIG. 15. Lessoniopsis, 30 mm., lamina showing the characteristic spots, midrib just beginning to appear, holdfast formed by conspicuous primitive hapteres.

FIGS. 16–17. Renfrewia, adult, showing similarity to Lessoniopsis when young, fruiting area covers almost the entire lamina in Fig. 16, but in Fig. 17 occupies only a small area at the base and hence clearly discernible, spots in Fig. 16, due to epiphytic algæ. About one half natural size.

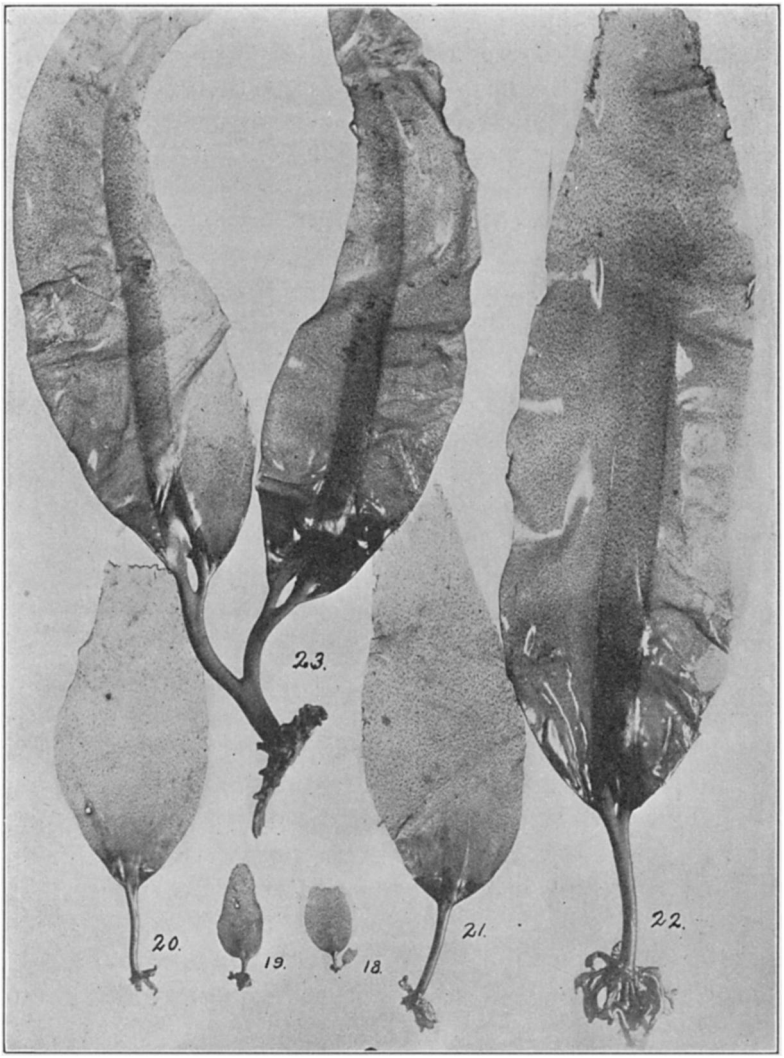
The base of the stipe was but slightly larger than the portion above and gave off a large number of filamentous processes, some of which seem to have pressed against the substratum, while others apparently connected with the filaments around the base. Notwithstanding its small size this specimen had a well-developed stipe about a dozen layers of cells in thickness. The internal cells are considerably elongated, though not, as far as can be seen by focusing, differentiated into a pithweb. The lamina was already several cells in thickness even at the edge. Since it was but little frayed, it hardly seems possible that there could have been any remnant of the one-layered lamina which had not been transformed into the many-layered adult blade. In this respect Lessoniopsis would stand at the opposite extreme from Cymathere, in which a large portion of the embryonic lamina is not changed, but continues to grow and persists until the plant is more than 20 cm. long.

The next larger specimen (Fig. 4) measures 2.3 mm., but its true length must have been about 5 mm., for it is sharply truncated a little above the base of the lamina. The holdfast of this specimen was enlarged to form a fairly well developed primitive disc, the base of which was, as in the first specimen, more or less imbedded in a mass of filaments apparently belonging to the kelp. The lamina was much thicker and the spots were seen to be in two layers, one on each side, just beneath the epidermis. In the smaller specimen (Fig. 3), where one spot overlapped another, the two layers could also be made out, but the difference in focus was so slight as to make it appear that they lay in contact, indicating that the lamina was four cells in thickness. In the larger specimen they were separated by a considerable interval which indicated a decided development of the pithweb and cortex. Toward the extremity of the lamina the pigmented spots were very dark and most of them were considerably elongated. They still consisted, however, for the most part, of single cells. Farther back in the transitional region, they were lighter in color, round and more

like those of the first specimen (see Fig. 3). This shows that the region of growth had been definitely localized as a meristem at the base of the lamina (as in the mature plant), while further out in the lamina growth was taking place mainly by the enlargement of cells already formed.

From this point on the development of the species was illustrated by many specimens of all ages. The first marked change was the enlargement of the primitive disc. In a specimen 30 mm. long (Fig. 15) the disc had reached a diameter of 4 mm. At this stage it bears a striking resemblance to that of the adult Renfrewia, being very flat and closely appressed to the substratum. As in that genus, the growth which causes the enlargement becomes localized in certain regions, giving the disc a crenate margin. In places the localization had become sufficiently pronounced to give rise to definite primary hapteres exactly as described by MacMillan ('99) for young plants of Nereocystis and by the writer in the adults of Renfrewia and Cymathere. These primary hapteres are of course all restricted to the primitive disc. Soon after this stage the secondary hapteres begin to arise around the base of the stipe and become very abundant, quickly obliterating the primitive holdfast. The age at which branching and differentiation of the midrib appear varies greatly. Sometimes the plant may reach a length of 80 mm., with only the beginnings of the midrib and of the splitting to form the first branch (Fig. 21); while in one plant of 160 mm. the perforation of the midrib for the branch had only just been accomplished (Fig. 22). On the other hand a specimen (Fig. 19) measuring only 18 mm. showed the position of the perforation plainly marked out. The first appearance of the midrib is indicated by two straight lines extending from the transition region up into the lamina (Fig. 20). The lamina between them grows thicker and takes on the characters of the midrib, which gradually extends toward the tip. But usually for a long time the two edges are more pronounced than any other portion of the rib.

As is well known, the whole subfamily, the Lessoniatæ,



FIGS. 18–23. Lessoniopsis. Four fifths natural size.

FIG. 18. Young plant at about the same stage as Fig. 15 to which is attached another intermediate between it and that shown in Fig. 4.

FIG. 19. Plant grown in heavy surf, holdfast very large; plant dwarfed, indentation for first branch already appearing in the transition region.

FIG. 20. Plant from quiet water grown to an unusually large size, with no indication of branching, midrib just forming.

FIG. 21. Similar to the last except for the beginning of the perforation.

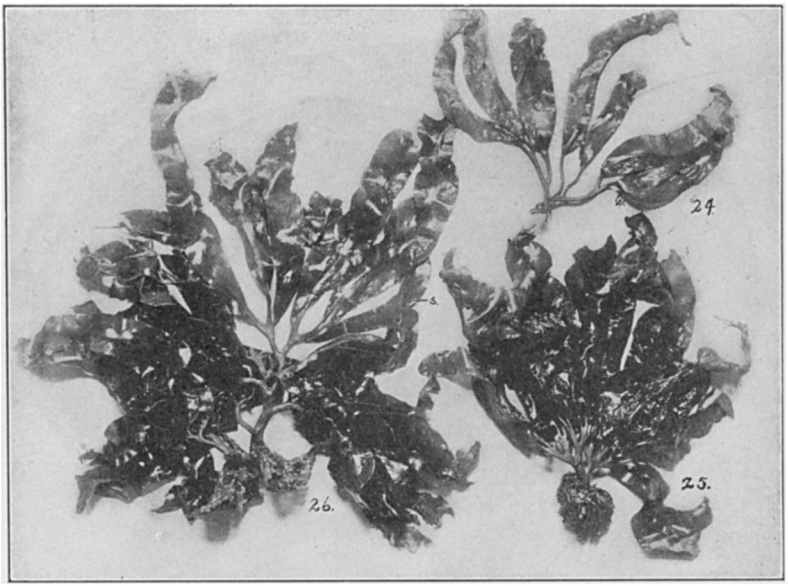
FIG. 22. Perforation complete.

FIG. 23. Primary branching complete, perforations formed for second branches, inner side of new laminæ beginning to form from the divided midrib.

to which Lessoniopsis belongs, is characterized by the repeated splitting of the original unbranched lamina till the plant comes to have a cluster of many leaves. The method of this branching is peculiar to the kelps. Instead of forking at the tip or sending out a new shoot as a lateral proliferation, the branching begins in the transition region between the stipe and the lamina and extends upward until it reaches the tip of the lamina, thus splitting it, while the stipe is divided, to a greater or less extent in the different genera, by the downward extension of the same process. This method of branching is the necessary consequence of the position of the meristem, which is situated at the junction of lamina and stipe, so that all new growth is intercalated between the older portions of both. It is obvious, therefore, that any new structure, such as a branch, must originate in this region of growth.

In Lessoniopsis the first indication of branching appears in a slight depression in the midrib on each side of the lamina at the transition region. These depressions or pits enlarge and deepen until they meet and form a perforation almost exactly at the base of the lamina. It will be readily seen that if the split extended uniformly upward through the midrib, it would result in two unsymmetrical falcate laminæ each with a rib along its inner side. This, however, is not usually the case, for new tissue forms between the divisions of the midrib and soon duplicates on the inner side the outer edge of the lamina (Fig. 24, *a*). Thus each of the new laminæ is approximately symmetrical with respect to its midrib. In the stipe the branching is carried far enough to involve the whole of the meristem, so that future lengthening is almost completely confined to the stipes of the branches.

Before the new laminæ have completely separated there usually begins to appear at the base of each, the second split, which is carried to its completion in the same manner as the first. Thus branching continues again and again so long as the plant lives. Since all the splitting is dichotomous, the result should be a flat fan-shaped plant,



FIGS. 24–26. Older Lessoniopsis. About one sixth natural size.

FIG. 24. Plant several times branched; at *a* the process of the formation of the inner side of the divided lamina from the midrib is clearly indicated.

FIG. 25. Plant with about 25 laminæ, original dichotomy plainly shown.

FIG. 26. Plant still undersized but with the characters of the adult; one branch is lifted out by a background to show the sporophylls (*s*) and their relation to the ordinary laminæ, which show the beginnings of division at their bases as in the younger forms.

and sometimes this form is attained even in very old plants, especially those growing in the quieter places, but usually the stipes twist more or less and spread out in all directions, giving the plant a tree-like aspect.

There is no change in this habit of growth until the plant has attained a considerable age. But long before it reaches its full size there appears another kind of lamina among the narrow ones with midribs. These lack the midribs and are much wider, with conspicuously rounded or subcordate bases. The ribbed laminæ are always sterile, but these wider ones become sporophylls. Consequently after their sporangia are discharged they slough off and disappear, leaving for a time scars on the stipe. The origin of these sporophylls is evidently different from that of the ordinary laminæ. Since very few new sporophylls are developed during the summer, at

least at Port Renfrew, it seems probable that their production is a seasonal phenomenon taking place only for a limited period before the fruiting season. However they are formed, they do not reach their full size at first. The youngest are always shorter and narrower than the older and entirely lack the characteristic base. Some of the smallest remind one of the young sporophylls of Pterygophora and have the appearance of being outgrowths from the meristem as in that species, but the writer does not feel sure that they are normal. Further information on the origin of the sporophylls will be very welcome because of its importance in determining the relationships of this plant to the other genera of kelps.

At length, by branching and production of sporophylls a plant is formed with several hundred laminæ, in extreme cases reaching lengths of a meter, while the whole plant is often two meters long. The stipe at the base becomes 10–20 cm. in thickness and is marked with many annual rings of growth. The holdfast clings so tenaciously to the rocks that it will support a man's weight. On a flat bottom the plants stand upright, but they hang down when growing on an overhanging cliff, as in the photograph (Fig. 27). As in all water plants, their only way of maintaining themselves in the strong currents in which they live is by bending before them. Accordingly, rigidity is developed only in very large basal portions of the stipe, while the terminal branches have not sufficient stiffness to support the plant when out of the water. Lessoniopsis thrives only in places where the surf is very heavy and is there found along with Postelsia, the sea palm, the most typical of all the cumaphytes, but it does not withstand drying so well as that plant and consequently grows at a considerably lower level.

C. *Egregia*

To one acquainted with the kelps only through the more widely distributed genera such as Laminaria and Alaria, Egregia must always be the most interesting of the family. Algologists agree in assigning to this plant the high-

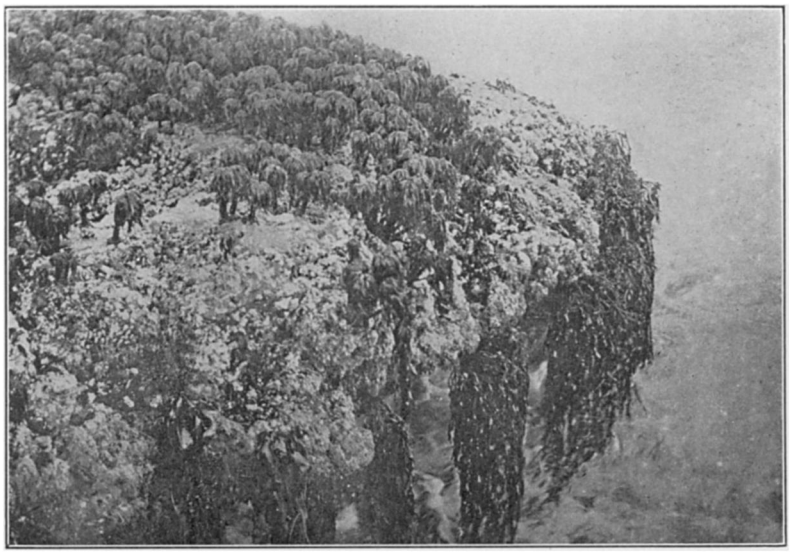


FIG. 27. Lessoniopsis (hanging) and Postelsia (upright) growing on an overhanging shelf exposed to the heaviest surf. Lessoniopsis is about two meters long and Postelsia, one half meter.

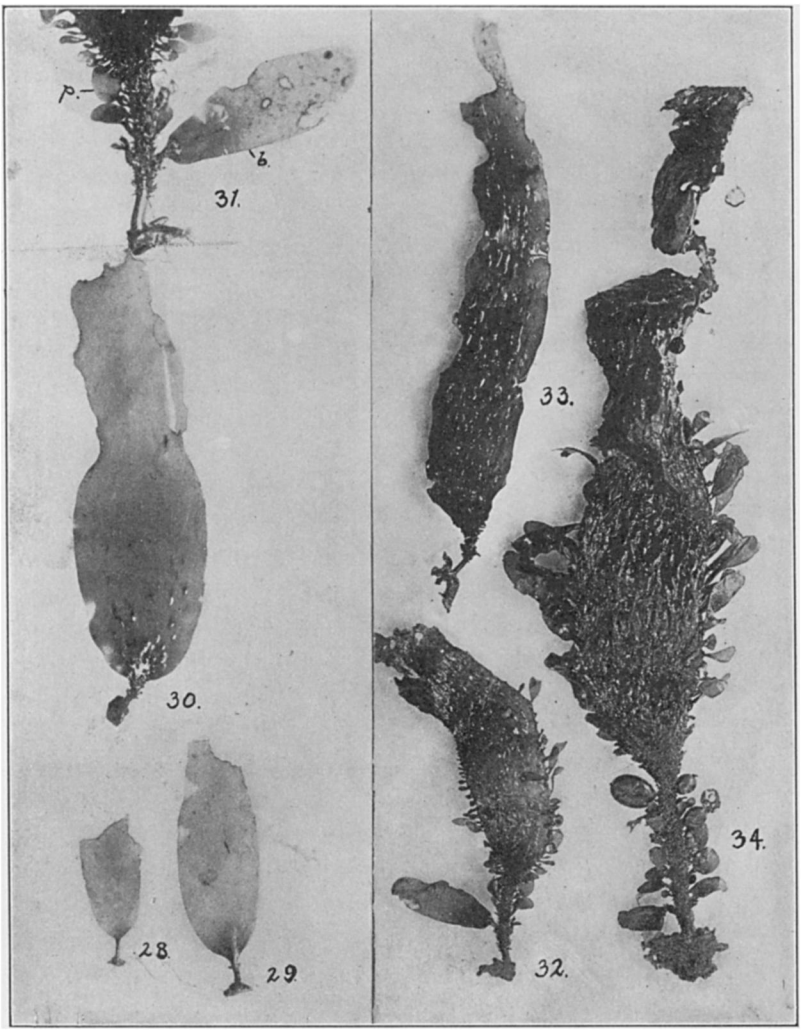
est place among the kelps as being the most specialized of them all. It is a genus of the western coast, represented by two species, one northern, the other southern. Both are extremely variable and in their many forms and intergradations present to the taxonomist a problem of more than usual difficulty. Some features of the morphology of the northern species, *Egregia menziesii,* have been presented in a paper by Ramaley ('03), illustrated with some excellent figures of adult and middle-aged plants, while Reinke ('03) has also given figures and a brief description of somewhat younger plants. The development of this species which grows abundantly at the Minnesota Seaside Station, will be worth considering in detail in connection with the other kelps discussed above because of its greater complexity.

Egregia, like Nereocystis, has an extremely long stipe; indeed, in proportion to its lamina its stipe is much longer, but its character is totally different from that of Nereocystis. In the latter plant the stipe stretches from the holdfast, frequently attached to a depth of twenty or

thirty feet, like an anchor rope, to the surface, where it holds the large float and laminæ against the impact of the heavy surf. This stipe is often less than one centimeter in thickness for half its length, but of such surprising strength that the native fishermen tie their boats to these ready-made anchors and ride out a storm, as noted by MacMillan ('99). The stipe of Egregia, however, while slender and flexible, is not bare, but covered with very numerous short proliferations along its whole length giving it the appearance of a feather boa. Some of these are photosynthetic areas, some sporophylls, some floats filled with air. The presence of such organs as air vesicles so near the holdfast shows clearly the plant's adaptation to a shallow-water habitat. It grows attached to rocks which are never deeply submerged and are uncovered even by a moderately low tide, where its branches, buoyed up by their innumerable pneumatocysts, float with their whole lengths on the surface of the water. To the boatmen along that shore a thick bed of Nereocystis is a sure sign of deep water, but a bunch of Egregia as surely marks a rock to be avoided.

The youngest plants of Egregia are extremely difficult to separate from those of Hedophyllum. The juvenile forms of both these kelps are dark brown, distinguished from most others of their size by shorter stipes, together with a rather strong development of hapteres. The youngest plant of Egregia found (Fig. 28) was 25 mm. long, with a lamina about 20 mm. long and 10 mm. wide. The holdfast had already developed a circle of secondary hapteres, although the primitive holdfast could be made out beneath the secondary. The stipe was but 3 mm. long, cylindrical, and featureless except for a very slight thickening about a millimeter below the base of the blade. This appeared to be the beginning of the proliferations which characterize the later stages of the plant.

The thickening of the stipe soon becomes more pronounced and develops into a pair of horns about a millimeter long just below the base of the lamina and lying in the same plane (Fig. 29). These are the only dis-



FIGS. 28–31. Egregia. Five sixtns natural size.

FIG. 28. Youngest plant, barely distinguishable from Hedophyllum at this age, cf. Fig. 37, which is less eroded.

FIG. 29. Plant showing the first pair of proliferations on the stipe.

FIG. 30. Plant with the transition region roughened by many capillary proliferations, tuberculate ridges appearing in the base of the lamina.

FIG. 31. Base of a much older plant showing the differentiation of the first branch (*b*) made evident by the appearance of proliferations on its stipe, first pneumatocyst (*p*) just appearing, base of stipe remaining smooth.

FIGS. 32–34. Egregia. One half natural size.

FIG. 32. Whole of the plant shown in Fig. 31, proliferations on the lamina absent at the tip, but well developed below.

FIG. 33. Much younger plant than Fig. 32, capillary proliferations prominent in the transition region, laminar proliferations just beginning to appear on margin of both stipe and lamina, tip of lamina smooth, other portions covered with protective ridges.

FIG. 34. Older plant in which the lamina has reached its maximum development and the stipe has begun to grow, several well-developed pneumatocysts and young branches are evident among the outgrowths from the stipe.

tinguishing features of the plant until it reaches a length of about 40 mm. In plants of about this length a few round tubercles begin to appear at the base of the lamina, which has hitherto been smooth as in Hedophyllum. A specimen 75 mm. long (Fig. 30) showed numerous tubercles in the transition region, giving it a roughened appearance; and there were three instead of two horns below the zone of the tubercles. The basal portion of the stipe was still smooth as in the youngest specimen. In this plant the stipe had elongated scarcely at all and the growth had been restricted to the lamina, which extended through 70 of the 75 mm. of the plant's length. Tubercles similar to those of the transition region had also appeared and these were shown by transmitted light to be connected with streaks of denser tissue running lengthwise through the lamina.

After this stage, as in Lessoniopsis there is some variation in the age at which the various structures appear. A specimen 18 cm. long (Fig. 33) will serve as an illustration of the next step. Here the streaks beneath the tubercles of the lamina had become prominent ridges, much larger than the small tubercles at their summits. The ridges stood out so strongly as to cause depressions on the opposite side of the lamina beneath them. This gave the lamina a wrinked appearance and added greatly to its strength. The margin was entire or slightly undulate, but at the base were a few short serrations which looked much like the tubercles of the stipe. The roughened region of the stipe was about 1 cm. in length and no longer terete like the lower smooth portion, but somewhat flattened. In place of the horns of the younger specimens were several outgrowths, the largest of which bore a small orbicular lamina. The holdfast had become nearly 2 cm. in diameter by the great elongation of a few hapteres.

In view of the proportions assumed by the adult plant the relation between the lamina and stipe in the juvenile forms is most interesting. In the smallest specimen the lamina is only about three times as long as the stipe.

But further growth is for a time almost restricted to the lamina until the ratio is increased to ten or fifteen to one. After this stage the stipe begins to grow and soon surpasses the lamina, which seldom exceeds half a meter in length, while the stipe sometimes becomes fifteen or twenty times as long.

A specimen 12 cm. in length (Fig. 32) though only two thirds as long as the one just described, was considerably more advanced. The uppermost quarter of the lamina was entire, as in the last plant, and below the tip were a few serrations like those at the extreme base of the former. Toward the growing point these outgrowths were larger and had become spatulate proliferations about a centimeter long, fringing the basal two thirds of the blade. The stipe had reached a length of 3 cm. Its numerous tubercles were much elongated and frequently dichotomously branched, once or even twice giving the peculiar roughened appearance characteristic of the adult. The proliferations along the lateral edges of the stipe were much more numerous than in the former specimen; some of them were simple laminar appendages; others were inflated into small globular pneumatocysts (Fig. 31, *p*); on others the stalks were roughened by small tubercles like those of the main stipe. Some of these last, if detached, might easily pass for young plants cut off just above the holdfast.

Though marked changes are yet to occur before the plant becomes mature, they may be understood by a comparison of the adult with this young plant (Fig. 32). The most conspicuous change is of course the great elongation. While this is especially noticeable in the stipe, the lamina likewise grows until it reaches a length of about 50 cm., but its width increases scarcely at all, seldom exceeding 4 cm. The proliferations from this narrow lamina become so numerous that they completely mask the distinction between it and the stipe, and it is only by close inspection that the lamina may be recognized. The growth of the stipe carries the lamina far away from the holdfast, where it is exposed to the severest action of the

waves, which lash the plant until the lamina together with the meristem is torn off and there remain simply the stipe and holdfast.

The stipe remains smooth for a few centimeters above the large branching holdfast, this being evidently a persistence of the smooth basal region of the young plant. Some of the lower tubercles, however, disappear, so that the smooth area now extends farther from the base than originally. This portion is terete, but at a length of about a decimeter the stipe becomes flat and strap-like about four times as wide as thick.

In the younger specimens the proliferations from the stipe and lamina are all small and not very numerous. In the adult they enlarge very greatly and increase in numbers so as to become by far the most conspicuous feature of the plant. The increase, both in number and size, is most marked toward the growing point, those at the base generally remaining small and scattered. Farther out along the stipe they are found of all lengths up to about 12 cm. and of various forms, as figured by Ramaley. They stand as thickly as possible along the stipe; in some places by actual count upwards of a hundred were found in a single centimeter of its length. Of these only a few were large and more than half less than a centimeter long. Crowded as they are along the edges of the stipe, they never arise from its faces, which are bare except for the tubercles described above. The air vesicles are formed at frequent intervals, providing sufficient buoyancy to keep the plant floating just beneath the surface with the tips of the proliferations emerging. When mature, they are about 30 mm. long, with an average capacity of about one cubic centimeter. Others of the outgrowths remain permanently small and become sporophylls. The outgrowths on the lamina also increase in size and number, but become neither so large nor so numerous as on the stipe. As noticed by Ramaley, no bladders nor sporophylls develop on the lamina.

Egregia becomes much branched before it is mature. Although Ramaley suggests that the branching may have

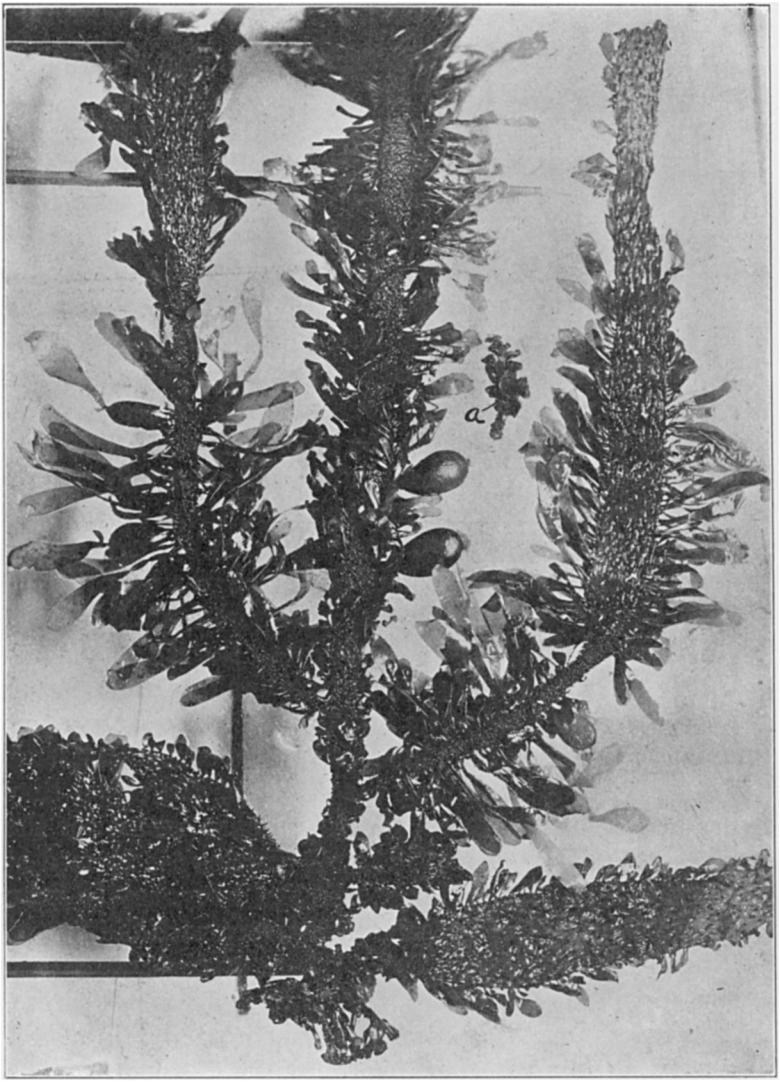


FIG. 35. Egregia, base of small plant with the characters of the adult except for the small number of branches, though only a few of those present could be shown, while the others were piled up in a mass to the left of the holdfast, (*a*) a dwarfed branch with a frilled margin. One fourth natural size.

an appearance similar to Lessonia, it is brought about by a fundamentally different process, as has already been noted by Setchell ('93) and by Reinke ('03), who figure several stages in the development of a branch. Some of the earlier proliferations, as stated above, soon develop roughenings on their stalks like those of the main stipe and take on the appearance of younger specimens of the species (Fig. 31, *b*). This is the first external indication of an important difference in the constitution of these outgrowths from the ordinary proliferations. For in them has become differentiated a meristem independent of that of the primary branch. They develop exactly as did the main axis and soon become indistinguishable from it except in the manner of attachment to the holdfast, possessing all the structures which have been described for a primary branch including other branches which in turn go through the same process. After several such branches have been formed there is a modification of the process. The laminæ are dwarfed, while their margins become conspicuously puckered and ruffled (Fig. 35, *a*). Sometimes the ruffles are so pronounced as to completely enfold the meristem. In such a branch proliferations from the lamina appear very late, but the ruffle gives it a similar aspect. The dwarfed condition of the laminæ persists until the stipes become several centimeters in length, when the usual relations of stipe and lamina become manifest. Though roughening may appear on other parts of the plant, the development of meristematic proliferations is confined to the basal portion; branches do not develop at a distance much exceeding 20 cm. from the holdfast. Around the base of any old plant there is always a large number of short branches in all stages of development, but there are not often more than a dozen long branches at any one time. The general appearance of the numerous dwarf branches suggests that they may not have a rapid development like the first branches, but rather grow very slowly or lie dormant for a time like the dormant buds of trees.

This method of branching is peculiar to Egregia and, as

FIG. 36. Egregia growing in a thick bed of kelp in which are prominent Alaria (with a midrib) and Hedophyllum (in foreground, especially at right).

far as the writer knows, nothing like it occurs in other kelps save in Thallasiophyllum. It is a matter of great interest from several points of view. Morphologically it gives the best reason for considering Egregia the highest of the Alariatæ, although that position would probably be accorded it without question because of the differentiation of the ordinary proliferations alone. The other members of this subfamily produce outgrowths which function as sporophylls, and in some of them, *e. g.*, Eisenia, these become the main photosynthetic areas of the plant. The development of meristems in such outgrowths, leading to the formation of branches, is the next step towards greater complexity and the logical summit of the Alaria series. But its greatest interest is from the ecological point of view. The extreme length of the stipe pushes the growing point far out, where it is lashed severely by the waves and frequently destroyed. Were the plant dependent on this for its continued healthy existence, as in Laminaria, it might easily be killed or at least handicapped for a considerable part of the time by the loss of the blade until a new one could be regenerated, as in many species of Laminaria. But, should the older branches be injured, these basal branches may develop at any time. By their

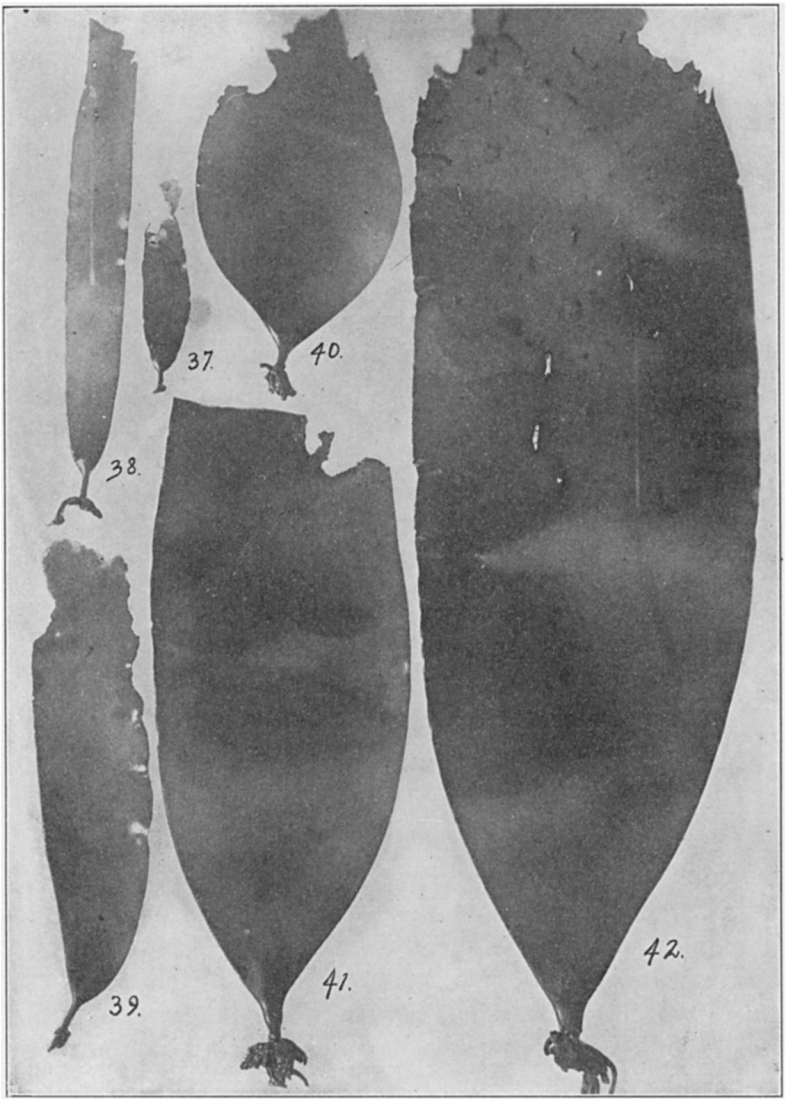
presence the plant is practically possessed of a new basal meristem supplementing and to a certain extent supplanting the primary meristem. Once established in a favorable situation, a plant may therefore maintain itself indefinitely, casting off old branches and developing new ones continuously.

D. *Hedophyllum*

Because of the close similarity of the young stages of Egregia and *Hedophyllum sessile* it will be of interest to add a short description of the latter. It has already been the subect of considerable study by Setchell, who has published ('05) a discussion of its development well illustrated by figures. His paper, however, was written from another point of view than the present, namely, the relationships of *Hedophyllum sessile* to the other species of Hedophyllum and to Agarum and Thalassiophyllum. Since from this standpoint the very young forms of Hedophyllum are not important, Setchell was not particular to obtain plants less than about 5 cm. in length. But for a comparison with Egregia the younger forms are of the most interest. This species[2] is extremely abundant at the Minnesota Seaside Station, outnumbering in individuals any other kelp present on that coast. It grows at the highest level occupied by the kelps, and in various situations as regards wave action.

Very young plants of Hedophyllum are difficult to distinguish with any certainty from Egregia and from the various species of Laminaria growing in the same locality. Hedophyllum is, however, much more abundant in adults and juvenile forms, and as the specimens selected were taken from beds composed mostly of Hedophyllum, the probabilities are greatly in favor of a correct determination. The youngest plant (Fig. 5) measured approxi-

[2] Though Puget Sound is given as the southern limit of the other American species, *Hedophyllum subsessile*, I have been unable to satisfy myself of its occurrence at Port Renfrew. Two distinct series of juvenile forms are, however, represented there, one with a narrow blade like those which Setchell figures, and, as here described, another with a very broad, cordate blade even when very young. What the relations of these may be to the adult plant I have not yet fully determined.



FIGS. 37–42. Hedophyllum, series of young plants showing the gradual obliteration of the stipe by the broadening of the transition region, and the origin of new hapteres higher and higher up the stipe. Four fifths natural size.

mately 2.3 mm. in length and the margin of the primitive disc was nearly smooth. The edge of the lamina was only one cell in thickness, but there were evidently several layers in the middle region and toward the base. In a specimen 6.5 mm. long the holdfast had become distinctly crenate around the edges and the one-layered lamina had disappeared. The crenations had become much more pronounced and had assumed the characters of primary hapteres in a specimen 10 mm. long (Fig. 6).

By the time the plant reaches the length of an inch its determination is not difficult. A specimen 28 mm. long (Fig. 37) will serve for comparison with the youngest Egregia described. The lamina is narrower and longer than in that plant; the holdfast has not as yet developed secondary hapteres and the stipe is shorter. Though the stipe always remains short, it usually becomes longer than is shown in this plant (about 5 mm.). The narrowness of the lamina is characteristic, but is not sufficiently marked at stages earlier than this to render diagnosis easy.

Soon after this stage secondary hapteres begin to appear above the primitive holdfast. Though they arise in circles as in the other kelps, they usually develop quite unevenly in the young plant, some members of the circle becoming long, while others are yet mere knots on the stipe. When a length of about 8 cm. is reached the stipe begins to thicken and flatten. The transition region, which has been sharply marked off, becomes less and less distinct and the plant comes to consist of a lamina with a cuneate base anchored by the holdfast (Fig. 42). This condition sometimes persists until the plant has reached a considerable size. More usually, however, the broadening continues and quickly brings about the adult condition.

When mature (Fig. 43), *Hedophyllum sessile* becomes a broad, cordate, sessile plant anchored by a mass of hapteres at its base. Its lamina is torn to ribbons like a digitate Laminaria, so that it may resemble one of the kelps with true branching. The hapteres arise in circles one above the other higher and higher up on the stipe

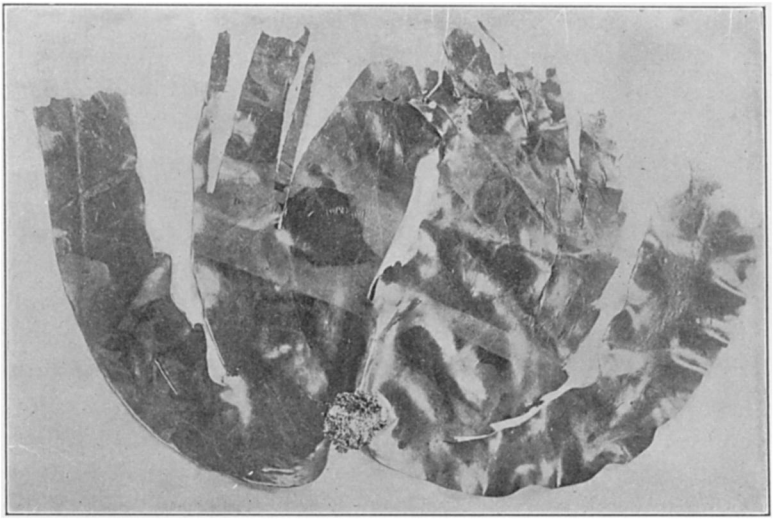


FIG. 43. Hedophyllum, medium-sized plant showing the cordate lamina torn by the waves. A fully mature specimen would be a rosette so dense that its structural relations could not be made out. One fifth natural size.

until they obliterate it and even come to grow out from the lamina itself. Thus there arises a thickened basal portion of the lamina which forms a conical holdfast, as in the other kelps, while new circles of hapteres may be seen on its upper edge, growing out from the undifferentiated lamina. By this process the holdfast region extends beyond the bases of the segments of the lamina so as to give the old plant the appearance, not of one, but of several independent laminæ springing from a common holdfast. Considering the similarity of the young plants to Egregia, the divergence of the adults is very striking.

(To be concluded)